The legs are also long and stout. The hind wings are absent, and are replaced by rather long tubercles, to the end of each of which is articulated a strong bristle, hooked at the tip, the tip fitting into a pocket on the hind border of the wings. The eyes of the male insect are very large and strongly faceted. The mouth parts are entirely absent, their place being taken by supplementary eye spots. The function of the male insect is simply to fertilize the female, and it then dies. The number of generations annually among bark lice differs so widely with different forms that no general statement can be made.

EMBRYOLOGY.[1]

The development of Isopods.—Last Winter when M. Louis Roule published a long paper in French on the development of an Isopod, *Porcellio scaber* Leach, it seemed advisable to present a rather full abstract in this magazine, for the benefit of those readers who would not see the original or who did not read French. That abstract appeared in February and contained, besides the descriptive account of the embryology, some interesting conclusions based on these results.

In the May number of the Journal of Morphology Dr. J. Playfair McMurrich publishes a long paper, illustrated with excellent figures, which is not at all reconcilable with M. Roule's views. It must be remembered, in comparing the two papers, that M. Roule studied a single species of Isopod, that he gives rather diagrammatic figures, and that his description of the segmentation, on which apparently the whole fabric rests, is of a very general nature.

Dr. McMurrich took up the work in 1890, hoping to make out the cytogeny of a Crustacean as Whitman had done for Clepsine, and as E. B. Wilson has later done for Nereis and other forms. This author's results rest then on a thorough study of the segmentation, and as he did not confine his attention to one form, but observed and figured the segmentation and early differentation in a number of Isopods, the paper is of especial interest.

The forms studied were *Jæra marina* Möbius (1873); *Asellus communis* Say; *Porcellio scaber; Armadillidium vulgare;* with some observations on *Cymothoa* and *Ligia.*

The segmentation is centrolecithal. The nucleus of the unsegmented ovum lies in a central mass of protoplasm surrounded by yolk, and

[1] Edited by E. A. Andrews, Baltimore, Md., to whom abstracts, reviews and preliminary notes may be sent.

from the central protoplasm a network extends out through the yolk to a peripheral layer. It is possible to determine the second plane of division as that of the long axis of the embryo as has been shown to be the case in Nereis, Crepidula, and Umbrella. In discussing the segmentation, the author uses the term cell as a convenient one for the nucleated bodies of protoplasm which appear on division in the yolk, but he insists on the syncitial nature of the ovum to a late period.

The cleavage is apparently a spiral one, and results in what may be spoken of as a blastula stage, in which considerable differentiation has taken place. From the eight cell stage, especially in Jæra, it is possible to trace the history of different areas of this blastula to certain well marked cells. For instance, in Jæra, a cell at the posterior pole gives rise to the future Vitellophags, three cells immediately encircling it are the ancestors of the mesendoderm, while the ectoderm arises from the remaining four anterior cells. There are some interesting variations in this history in the forms studied, though the end result is practically the same. The author concludes with E. B. Wilson that, "cells having precisely the same origin in the cleavage, occupying the same position in the embryo, and placed under the same mechanical conditions may nevertheless differ fundamentally in morphological significance."

In connection with the segmentation Dr. McMurrich thinks that the existence of a syncitium up to so late a period in differentiation is of special interest in relation to the current disscusion of the cell-theory. The question is asked, "are we to believe that there is no continuity in Lucifer, between the blastomeres, notwithstanding that in all probability there was continuity in the ova of its ancestors?" In *Peripatus capensis* there is an approach to holoblastic cleavage associated with less yolk and still a syncitium results. This is regarded as supporting "the supposition that, even in such cases as Lucifer, there may be also a continuity of protoplasm, the separation into distinct spherules being only apparent."

It should be remembered that, however, plausible this argument is, of course the fact of continuity between the blastomeres of Lucifer or of other holoblastic ova still remains to be proven by direct observation.

The conclusion that "the existence of a syncitium is no bar to a certain amount of differentiation," certainly seems justified from the facts described for Jæra. Continuing this subject, such a syncitium is compared with the differentiation in certain protozoa, and a peculiar phenomenon in Porcellio is considered, where there is a precocious segregation of a portion of the cytoplasm which is to take part in the

formation of the blastoderm. This segregation is said to take place, "not in accordance with any previous location of a nucleus, but independently." Dr. McMurrich thinks that "this phenomenon seems to demonstrate that cytoplasmic differentiation may occur *independently of definite nuclear influence.*" He immediately adds, however, that "he, of course does not mean to assert that the nuclei may not possess a *coördinating or even a trophic action upon the cytoplasm,* but that they are directly responsible for the segregation or concentration seems to him an unwarranted assumption."

It is difficult to understand just what is meant by these statements. The remarkable concentration of the peripheral protoplasm of the ovum of Porcellio toward the definitive ventral side, independently of any previous location of nuclei, is notewothy. Does it, however, "demonstrate cytoplasmic *differentiation* independent of definite nulcear influence?" Can this *movement* of protoplasm, even toward a definite point, be correctly spoken of as *differentiation* and compared with the specialization in the cytoplasm of certain protozoa? Having in mind the condition of the ovum when this phenomenon takes place, is it not possible that the movement may be the result of nuclear influences from the center, acting through the central network on the periphal protoplasm?

Again, if the phenomenon demonstrates cytoplasmic differentiation *independent* of definite nuclear influence, why does the author add that, "he does not mean to assert that the nuclei may not possess a *coördinating* action upon the cytoplasm?" There seems to be a contradiction in these two statements, which may destroy the force of the argument. It should also be remembered that in Jæra, and in the other Isopods studied, there is a contraction of the blastoderm cells toward the ventral surface. Here the nuclei, as well as the cytoplasm, of the blastoderm are evidently directly involved. Perhaps the precocious segregation of cytoplasm ventrally in Porcellis is but an early appearance of this process. If it be admitted that the nuclei possess coördinating influences on the cytoplasm, how can it be claimed that in the case of the highly differentiated protozoa such influences were not active during the differentiation?

Another point discussed is the extent of external influences and their action, in holoblastic and in centrolecithal ova like those of Jæra. The conclusion reached from a review of the facts of segmentation is that "the cleavage form of Jæra is determined entirely by intrinsic conditions." The phenomena of segmentation "leave us no choice but to refer the vis essentialis which determines the direction of the Karyokinetic

spindle, and therefore, the cleavage form of Jæra, to the constitutional peculiarity of the ovum." "Holoblastic ova, the author believes, can not be excluded from the action of external forces, but the presumption is allowable, for several reasons, that even in these intrinsic forces are important." The assumption must consequently be made "that intrinsic forces reside in all ova, though they may be overshadowed by external influences in some cases."

It is important to examine the assumption which forms the foundation of this argument. The author quotes E. B. Wilson's conclusion that "cleavage forms are not determined by mechanical conditions alone," and assumes that by "mechanical conditions," Wilson means conditions extrinsic to the ovum. This can hardly be so, for it is necessary to include among the "mechanical conditions" influencing the cleavage of an ovum like that of Jæra, the presence in the cytoplasm of a great accumulation of food-yolk, (excessive in quantity when compared with that in holoblastic or meroblastic ova). It is true that this mass is within the ovum, and in so far "intrinsic", but its action is usually looked on as that of a foreign body, so to speak, which modifies and obscures the primitive phenomona of cleavage and differentiation as seen in holoblastic ova. Hence it is important to remember that Dr. McMurrich, in maintaining that "the cleavage form of Jæra is determined entirely by intrinsic conditions," must include the action of the nutritive mass. This would seem to weaken materially the position that extrinsic influences, (in the generally accepted sense as extrinsic to active cytoplasm), are excluded from action on the spindles of centrolecithal ova. The confusion seems to lie in the use of the word intrinsic to include, in the case of the ovum of Jæra, both inherent properties of the protoplasm, and secondary forces due to the presence of a body of nutritive material which is morphologically not a part of the protoplasm. Dr. McMurrich's conclusion, that "instrinsic forces reside in all ova", or preferably, as E. B. Wilson has just it, "cleavage forms are not determined by mechanical conditions alone," will probably be accepted as truth by most observers. However, I can not see that he has shown that "in Jæra we have practically a demonstration of the correctness of this view" of a more convincing character than is exhibited by holoblastic ova.

"The cleavage form of Jæra, is said to be, determined entirely by intrinsic conditions." A conclusion from which Dr. McMurrich sees no escape, after a review of the changes of position in the yolk assumed by the nuclei during segmentation. The Karyokinetic spindles then are regarded as entirely beyond the influence of forces external to the

ovum in such eggs as those of Jæra, and their direction, with consequently the cleavage form, is due without other alternative entirely to the constitutional peculiarity of the ovum. After carefully considering the evidence presented by Jæra and similar centrolecithal eggs, the assumption does not seem warranted, that they are any more removed from the influences of external forces, than are holoblastic ova. It may be true that it is difficult to *understand* how forces external to a centrolecithal ovum may affect the spindles within it, but many will find the same difficulty in the case of holoblastic ova. Does the great increase of yolk in a centrolecithal ovum remove the spindles from the action of the external world? I, for one, can not see that this necessarily follows, and hence do not see that the condition of segmentation in Jæra leaves us no escape from the conclusion that its cleavage form is determined entirely by intrinsic conditions.

Returning to the description of the embryo, it will be remembered that the germ-layers are already distinguishable in a blastula stage on the surface of the yolk in Jæra, and somewhat less distinctly in the other forms. Now the blastoderm cells gradually concentrate towards the ventral surface of the egg. This results in the mesendoderm and vitellophag cells being crowded beneath the surface in the form of a solid plug, and in the ectoderm of the ventral surface marking out a somewhat triangular area, the base of which lies anteriorly while the apex is posterior. This area is the Nauplius region. The rudiments of the eyes are placed anteriorly at the angles of the base, the appendages appear later along the sides, while the blastoporic plug of mesendodermal cells lies just under the posterior apical end. In a most interesting discussion of the formation of the germs layers in the Crustacea, the author concludes that the primitive Crustacea probably passed through a blastula stage which was filled with yolk, and in which a plug of cells migrated into the yolk to be later differentiated into mesoderm and endoderm. This is the condition exhibited by the Phyllopods (Samassa, 1893 and Bauer, 1892). Jæra, the Decapods and especially Lucifer are examples of precocious differentiation of the germ layers. The entire mesendoderm of Crustacea has a blastoporic origin, and is not (except in Decapods, where there are secondary phenomena) formed by delamination of extra-blastoporic region. The under layer of the latter regions is formed by a migration of cells from the blastoporic plug. In Armadillidium this is especially well made out. An interesting question is raised in regard to the mesenteron of Astacus. Dr. McMurrich suggests the probability that the yolk-pyramids do not form it, but eventually form mesodermic tissues, while

the mesenteron is really formed by cells of the entodermic plates. This interpretation would be more in line with what is known of other Crustacea. Some of the most interesting observations and conclusions of the paper are those concerning the development of the metanaupliar regions of the embryo. It is a remarkable fact that the Naupliar and more posterior metanaupliar regions are very sharply distinguished by differents methods of growth. Dr. Patten was the first to call attention to the fact of teloblastic growth in the ectoderm and mesoderm of Cymothoa. Dr. McMurrich has gone further, and in his comparative study, has made out in detail the character and limits of this method of growth in Isopods. While the Naupliar is formed as described, the metanaupliar regions, are the result of teloblastic growth in ectoderm and mesoderm, just as the metatrochophoral regions of Polygordius are due to a similar process. The author is inclined to regard these two instances of teloblastic growth as acquired independently. He thinks that in the Isopod "the development points back to a period where a free-swimming Nauplius occurred in the development of the ancestors of the group, the egg embryo being a nauplius." At such a time the metanaupliar regions were developed after hatching. Now, however, this posterior region is developed in Isopods before hatching, but it still retains the peculiar teloblastic method of development, and is sharply distinguishable from the Naupliar area.

There is unfortunately not space to describe this remarkable process. It is interesting to note, however, that, while the ectoderm of the metanaupliar regions arises from the successive divisions of a row of ectodermal teloblasts, the rythm of these divisions is not the same as that of the row of mesodermal teloblasts which lies beneath. The mesodermal teloblasts divide just 16 times giving rise to 16 transverse rows of mesoderm cells, "each of which rows is equivalent to a segment," as is proved on the appearance of appendages. The ectodermal teloblasts divide twice as many times.

Though these are the main points of the paper, a number of important observations and conclusions have been necessarily crowded out of this review. For instance, I have not touched on the processes of impregnation, the formation of membranes, the details of segmentation and differentiation, the formation of the digestive tract, the history of the vitellophages, or the development of certain organs.

—H. McE. Knower.